STATE-DEPENDENT AND RISK-SENSITIVE ESCAPE DECISIONS IN A FOSSORIAL REPTILE, THE AMPHISBAENIAN *BLANUS CINEREUS*

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Morphological adaptations of amphisbaenians to fossorial life may affect their anti-predator behaviour and escape decisions. Amphisbaenians exposed on the soil surface by a predator may decide to escape either by burrowing immediately or by using alternative defensive behaviours. This decision may depend on the internal state (body temperature and associated burrowing performance) but, because anti-predator behaviours may be costly, an optimal response should also be sensitive to risk and vary according to the threat of predator attack. In a laboratory experiment we simulated predatory attack on individual amphisbaenians of the species *Blanus cinereus*, and specifically examined the effects of temperature (warm vs. cold) and predation threat (low vs. high) on escape decisions. Amphisbaenians showed significantly longer episodes of an alternative anti-predator behaviour on the soil surface (coiling) when the predation threat was high and when the temperature was low. The time to burrow until half of the body was buried was significantly longer when the temperature was low and was significantly shorter when the threat was high. The variations observed in anti-predator behaviours may reflect the choice of the optimal response under each circumstance, taking into account the estimated predation risk, which is dependent on the characteristics of the initial attack, and potential burrowing performance, which is dependent on body temperature.

Key words: predation, escape behaviour, fossorial reptile, *Blanus cinereus*

INTRODUCTION

Variation in external ecological conditions and in the internal state of animals may affect the costs and benefits associated with different behaviours. Avoiding predation is crucial for the survival of any organism (Lima & Dill, 1990). An animal that detects an approaching predator needs to decide whether to retreat to a safer location and, if so, when and how to escape. This is a clear example of a decision involving several costs and benefits (Ydenberg & Dill, 1986). Under these circumstances, trade-offs and decision rules (Bouskila & Blumstein, 1992), which are sensitive to internal and external conditions, are likely to be involved.

In surface-dwelling reptiles this cost-benefit analysis, and consequently the escape decisions, may be influenced by several factors such as distance to shelter (Cooper, 1997a), microhabitat (Martín & López, 1995b; Smith, 1996), age (Martín & López, 1995a), sex and reproductive state (Smith, 1996). The effect of body temperature has also been frequently analysed in reptiles because it has important implications for many aspects of their physiology such as, for example, their locomotory performance (reviewed in Huey, 1982). As a result, the ability of reptiles to escape is also affected by their internal thermal state (e.g., Rand, 1964; Hertz, Huey & Nevo, 1982; Arnold & Bennett, 1984; Passek & Gillingham, 1997). In addition, lizards (Burger &

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Gochfeld, 1990, 1992; Martín & López 1996; Cooper, 1997b), snakes (Bowers, Bledsoe & Burghardt, 1993) and other animals (e.g., Burger & Gochfeld, 1981) may react differentially to the approach of a predator as a function of the perceived threat of attack. Approaching predators do not always pose an immediate threat, and thus animals should tend to optimize the magnitude of their escape and anti-predatory responses accordingly, saving time and energy.

Amphisbaenians are a group of reptiles morphologically and functionally adapted to a fossorial life (Gans, 1978). Morphological adaptations to burrowing include trunk elongation, modification of the head size and skull, reduced vision and loss of limbs (Gans, 1978). These adaptations constrain amphisbaenians to solve their ecological demands with a suite of original responses different from those of other, surface-dwelling reptiles (Martín, López & Salvador, 1990, 1991; López & Martín, 1994; López & Salvador 1992; López, Martín & Salvador 1991; López, Salvador & Martín, 1998). Adaptations to fossorial life might also affect their anti-predator behaviour and escape decisions. Although predation pressure is apparently lower in the underground environment, there are some specialized predators, such as the wild boar and the Egyptian mongoose, which habitually dig extensive areas of soil or lift stones looking for prey and can leave amphisbaenians exposed on the soil surface (Busack, 1978; Martín & López, 1990). In these circumstances, amphisbaenians can escape either by burrowing immediately or by using alternative defensive behaviours on the soil surface, such as being immobile and cryptic or

showing saltatory coiling behaviour (review in Greene, 1988). This decision may depend on the internal state (body temperature) and associated burrowing performance, but an optimal response should also be risk-sensitive and vary according to the level of threat of predator attack.

We hypothesized that if the burrowing performance of amphisbaenians is better under favourable thermal conditions (i.e. optimal body temperature), amphisbaenians will tend to use alternative anti-predator behaviours to escape when thermal conditions are unfavourable. Additionally, because anti-predator behaviours and burrowing may be costly, the magnitude and characteristics of the escape response should be optimized according to the predation threat level by balancing the fitness effects of avoiding predators and saving energy.

In order to understand the reactions of fossorial reptiles to predation risk, we studied in the laboratory the burrowing escape behaviour of the amphisbaenian *Blanus cinereus*, using a multi-factor experimental approach. We aimed to identify the effects of variations in internal thermal state and in predation risk levels on amphisbaenians' escape decisions.

MATERIAL AND METHODS

The amphisbaenian *B. cinereus* is a fairly abundant fossorial species widespread in Spain. It lives in areas with sandy soils or abundant leaf litter, where it is usually found under rocks (Martín *et al.*, 1990, 1991). During March and April 1997, we captured adult *B. cinereus* (snout-vent length, SVL, males: mean±SE = 203±4 mm, *n*=12; females: 194±4 mm, *n*=13) by lifting stones in an oak forest near Navacerrada (Madrid Province, Central Spain). Amphisbaenians were kept individually in outdoor 5 litre cages with sand substrate from the capture area at "El Ventorrillo" field station (5 km from capture site). Amphisbaenians were fed mealworm pupae (*Tenebrio molitor*) and adult ants (*Pheidole pallidula*) twice weekly. Humidity was enhanced daily with a water spray. The photoperiod and the ambient temperature were those of the surrounding region. Amphisbaenians were held in captivity for at least one month before testing to allow acclimatization to laboratory conditions. All the animals were healthy during the trials and were returned to their exact capture site at the end of the experiments.

We measured anti-predator behaviour and burrowing escape performance of individuals by simulating a predatory attack on a buried individual that was extracted from the soil, handled and left exposed on the surface. Tests were performed in an experimental terrarium (100 x 50 x 40 cm) filled with a sand substrate from the capture area, under two different internal thermal states (i.e. cold vs. warm body) and two different levels of predation risk (i.e. threat of attack). Each individual was tested in all conditions under a randomized sequence, but it was used only once in each trial to avoid stress; the escape trials were spaced sufficiently (at least one day) that fatigue resulting from one test would not have affected subsequent tests.

To obtain differences in temperature conditions, amphisbaenians - buried in sand in their cages - were preheated or precooled by placing them in a constant temperature cabinet, together with the experimental terraria. We monitored substrate temperature (T_s) during the escape trials to ensure that thermal conditions did not vary during a test. The substrate temperatures of the cages were on average 31.1±0.1 °C in the warm condition and 16.9±0.2 °C in the cold condition. During preliminary tests we recorded body temperatures (T_b) of amphisbaenians and compared them with T_s. Body temperatures were highly correlated with associated T_s (r=0.97; P<0.001). On average, however, T_b was about 0.5°C higher than T_s, suggesting that amphisbaenians may achieve some limited physiological control over their T_b (Martín *et al.*, 1990; López *et al.*, 1998). This relationship was also similar to that found in free ranging *B. cinereus*, whose mean field body temperature was 22.2°C (Martín *et al.*, 1990).

Amphisbaenians were observed individually. To begin a trial, we took one buried individual amphisbaenian from its cage, simulating a predatory attack (e.g. a wild boar, that would have captured an amphisbaenian by digging the soil where it was buried). Because amphibaenians have very reduced vision, we assumed that they assess threat level as a function of duration and intensity of tactile contact. Thus, we either handled an amphisbaenian once, briefly and gently, and then released it (low predation threat level), or we handled it for a few seconds and, after an initial release, we simulated five more attempts at capture by tapping the amphisbaenian´s body with the hand (high predation threat level). We finally left the amphisbaenian on the soil surface in the middle of the experimental terrarium and recorded its behaviour without further handling. Experiments were recorded from above on videotape (Hi-8 format, 40 ms per frame) using a video-camera aligned perpendicularly to the terrarium. Timing and characteristics of the defensive and burrowing escape responses were accurately measured with a frame-by-frame analysis of the videotapes.

The repertoire of defensive displays of amphisbaenians has been qualitatively described elsewhere (Kenneweg, 1956; Van den Elzen, 1980; Malkmus, 1982; Greene, 1988). When released on the substrate, an amphisbaenian typically exhibits the following sequence of defensive behaviours, with variable duration: (1) it forms with the body a spiral, circular or sometimes a "pretzel-shaped" coil, then uncoils and reforms the coil ('Coiling'); (2) it remains still, apparently cryptic but not rigid or unresponsive, and occasionally forms a knot around a stick, or covers the head with a coil ('Still'); (3) the amphisbaenian uncoils the body, adopts a normal posture and moves slowly on the soil surface with undulate concertina movements of

TABLE 1. Results (*F* values) from independent two-way repeated-measures ANOVAs examining effects of temperature (cold vs. warm), predation threat (low vs. high) and temperature x threat interaction, on defensive and burrowing times of amphisbaenians. *P<0.05, **P<0.01, ***P<0.001; df=1,23 for all tests.

	Temperature	Predation threat	Interaction
Defensive:			
Coiling	10.99**	20.79***	2.93
Still	8.07**	0.42	0.33
Search	4.94*	0.08	0.62
Burrowing:			
Half-body	15.17***	5.30*	0.53
All but tail	18.15***	1.37	1.03

the body while, apparently, searching for a place to burrow ('Search'). After a period of searching, the amphisbaenian switches to burrowing at the chosen location. We noted the occurrence of these behaviours and measured the time amphisbaenians spent in each to the nearest second. We also measured the burrowing time, which we divided into three partial burrowing times: (1) time from initiation of burrowing until half of the amphisbaenian's body was buried under the soil surface, (2) time until all the body except the tail was buried and (3) time until the total length of the body was buried. Because amphisbaenians often stopped burrowing for long periods when part of their short tail

(tail length: mean±SE = 22.5±2 mm) was still on the surface, we used only the first two partial times in our analyses.

Previous analyses showed no differences between sexes in defensive and burrowing performance, so we considered males and females together. We used repeated-measures two-way analyses of variance (ANOVAs) (Sokal & Rohlf, 1995) to test for differences in each of the defensive and burrowing times of the same individuals in each condition of temperature (cold vs. warm) and predation threat (low vs. high) (within-subjects factors). We included the interaction between temperature and threat to determine whether responses to different threats changed under different thermal conditions.

RESULTS

Amphisbaenians showed significantly longer episodes of coiling behaviour when the predation threat was high and when the temperature was cold (Fig. 1, Table 1). Temperature did not significantly affect how coiling behaviour varied in response to different threats, as shown by the non-significant interaction term. Still and searching behaviours were of significantly longer duration at cold temperatures, but were not affected by predation threat.

Burrowing times were significantly longer at the lower temperature than at the higher temperature (Fig. 2, Table 1). The predation threat significantly affected only the time that an amphisbaenian spent burrowing until half of its body was buried in the substrate;
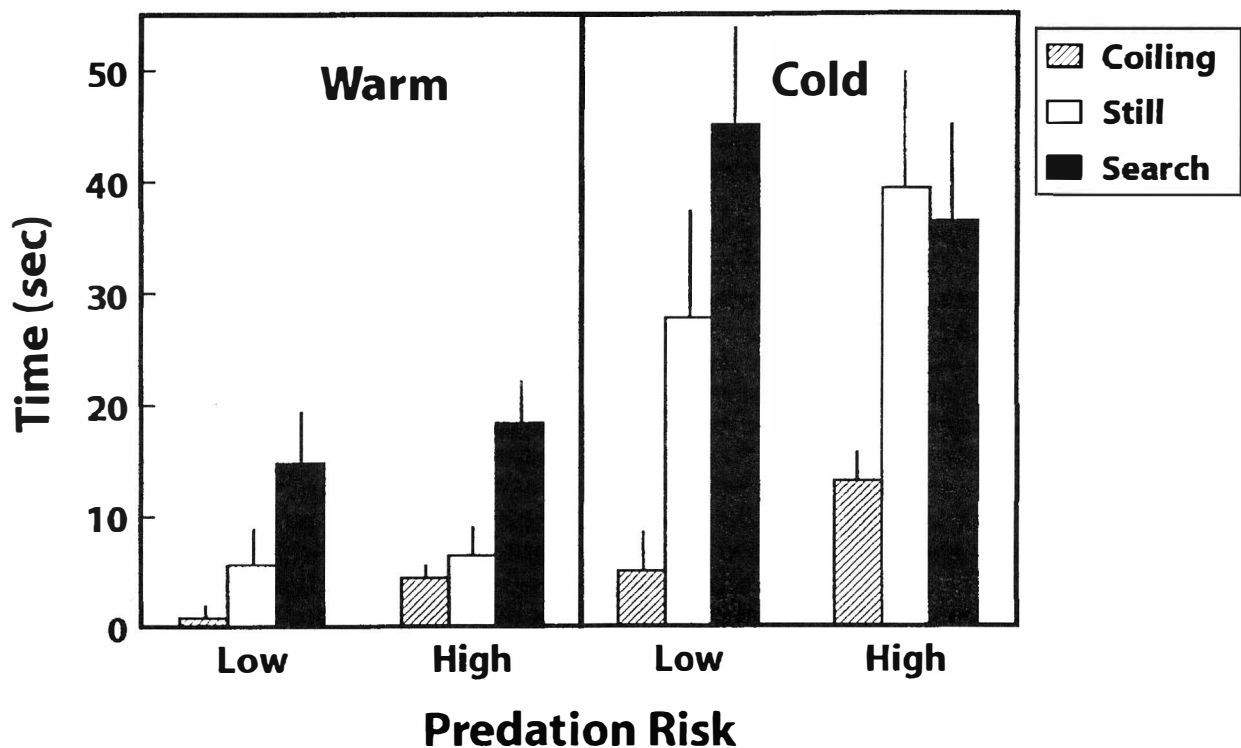

FIG. 1. Time (mean + 1 SE) spent performing each of two consecutive defensive behaviours (coiling and still) and in searching on the soil surface, by the amphisbaenian *Blanus cinereus* under two temperature conditions (warm vs. cold) and two different levels of predation threat (low vs. high).
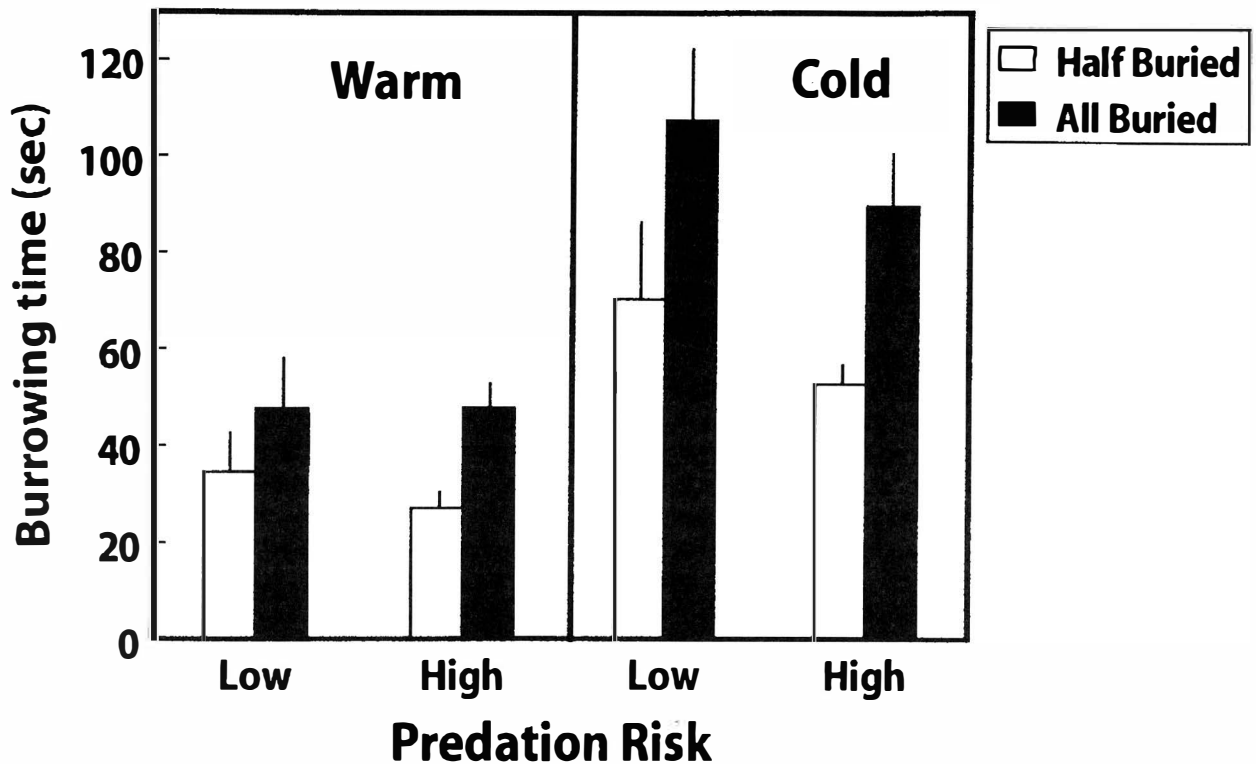
FIG. 2. Time (mean + 1 SE) from initiation of burrowing until half of the amphisbaenian's body was buried under the soil surface, and time until all the body except the tail was buried, under two temperature conditions (warm vs. cold) and two different levels of predation threat (low vs. high).

amphisbaenians burrowed significantly faster when the predation threat was high. The time spent burrowing until only the tail was left out of the substrate was also significantly longer at the lower temperature, but it was not affected by predation threat.

Of the 25 amphisbaenians tested under warm conditions, most of them burrowed until only the tail was left on the surface and then continued until all the body was entirely buried in the substrate (24 and 25 for low and high threat respectively). Under colder conditions, although most individuals also burrowed until only the tail was left on the surface (23 and 21 for low and high threat, respectively), only 17 and 18 (for low and high threat, respectively) completed the burrowing sequence during the experimental period.

DISCUSSION

The results of our experiment show that the antipredatory response of the amphisbaenian B. cinereus is affected by the internal thermal state and that it is also sensitive to predation risk levels. The variations observed in anti-predator behaviours may reflect the choice of the optimal response under each circumstance, taking into account factors such as the perceived predation risk, which is dependent on the characteristics of the initial attack, and potential burrowing performance, which is dependent on body temperature.

The amphisbaenians responded to an increase in predation threat by spending more time in coiling behaviour. They also increased the magnitude of this response (i.e. a faster and more vigorous formation of the coil). Coiling is a behavioural response of many limbless reptiles to attempted predation (e.g. Gans, 1974; Bauer, 1986; Greene, 1988), and appears to be a mechanism for startling or disorientating potential predators and eliciting misdirected strikes, rather than just a way to escape and move to safety. Because, in the high threat situation, we simulated repeated predation attempts, an amphisbaenian might perceive that the potential predator was trying to capture it directly rather than just touching it casually (i.e. low threat situation). Thus, an amphisbaenian should exhibit behaviours that would allow it to avoid an immediate capture. In contrast, escape by burrowing would not be as effective when a direct attack has already been launched, because it requires more time and because an amphisbaenian burrowing in a fixed place would be easier to capture. Similarly, coiling and other defensive behaviours were more often shown under cold conditions, when burrowing performance was lower. Nevertheless, although temperature was probably the main factor affecting burrowing speed, amphisbaenians that had faced a higher predation threat subsequently also burrowed faster, at least until half of their body was buried.

Temperature clearly affected burrowing performance of amphisbaenians, and this may help to explain the differences observed in defensive behaviours. Many lizards (Rand, 1964; Hertz et al., 1982; Crowley & Pietruszka, 1983) and snakes (Arnold & Bennett,

1984; Hailey & Davies, 1986; Passek & Gillingham, 1997) have different defensive behaviours depending on their body temperature. Warmer animals tend to flee from a potential predator, whereas colder animals will tend to remain and perform a more static defensive behaviour. The movement that a cold ectotherm is capable of may not be sufficient to escape from a predator, and so it should put its energy into alternative static behaviours that may serve to avoid capture (Passek & Gillingham, 1997). Thus, immobility may be an optimal alternative defensive behaviour for amphisbaenians when burrowing performance is low and costly (Kamel & Gatten, 1983). Immobility may benefit amphisbaenians by increasing their ability to avoid detection by predators, or by reducing the severity of the attack once detection has occurred (Brodie, Johnson, & Dodd, 1974; Greene, 1988). In addition, immobile amphisbaenians often form a knot in some part of the body around some stick or grass-stem (see photographs in Van den Elzen, 1980; Malkmus, 1982). This defensive strategy, which is followed by body rigidity, using axial bending when grasped, and by pressing the sharp tip of the tail against the predator, simulating a counter-attack, makes capture and consumption by a potential predator more difficult.

In conclusion, when thermal conditions were unfavourable or the predation threat was high, amphisbaenians employed alternative defensive behaviours before escaping by burrowing. These variations in anti-predator behaviours may reflect the choice of the optimal response under each circumstance.

ACKNOWLEDGEMENTS

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